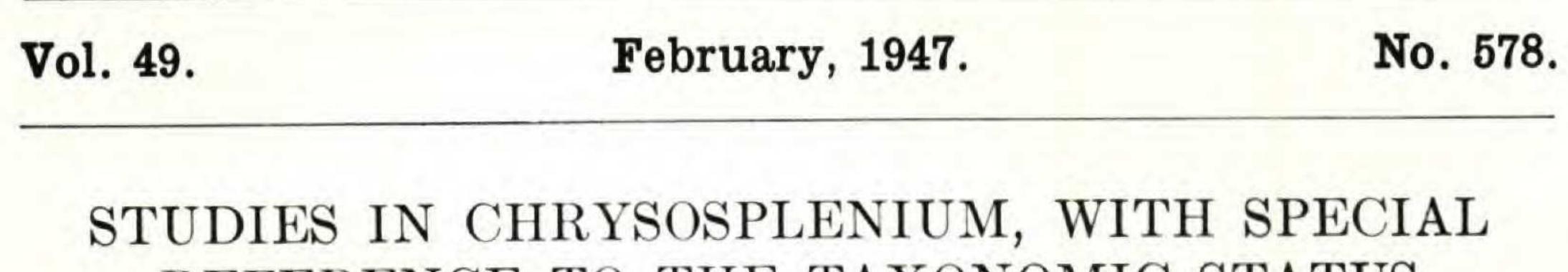
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STUDIES IN CHRYSOSPLENIUM, WITH SPECIAL REFERENCE TO THE TAXONOMIC STATUS AND DISTRIBUTION OF C. IOWENSE*

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(Plates 1053 and 1054)

SEVERAL years ago Professor E. H. Moss of the University of Alberta sent me a number of Canadian Saxifragaceae for identification. Among them was a specimen of Chrysosplenium (Moss, No. 280) which I referred to C. tetrandrum Fries. I made note of the fact that the number of stamens was not constant, but varied mostly between 8 and 6. This is one of the characters Rydberg¹ used for distinguishing his C. iowense from C. tetrandrum which, as the name implies, has only 4. I had not been fully convinced that this was a sufficiently reliable character for maintaining the former as a separate species, especially since a number of botanists dealing with Chrysosplenium from the Arctic regions of both the New and the Old World have reported finding plants of C. tetrandrum in which the stamens varied in number from 4 to 8. Some of them, particularly Simmons² and Heintze³, have emphasized this feature in support of their arguments that C. tetrandrum is only an Arctic variety of C. alternifolium L. They contend that such plants constitute a "con-

tinuous series" bridging the gap between the two.

* Contributions from the Herbarium of the University of Minnesota, III. ¹ Britton's Manual, p. 483. 1901.

Simmons, H. G. The Vascular Plants in the Flora of Ellesmereland. Rep. of the Second Norw. Arctic Exped. in the "Fram" 1898-1902. No. 2, p. 59, 1906.
³ Heintze, Aug. Om Chrysosplenium alternifolium L. v. tetrandrum Lund och des usbredning inom Skandinavien. Bot. Notiser, p. 231. 1907.

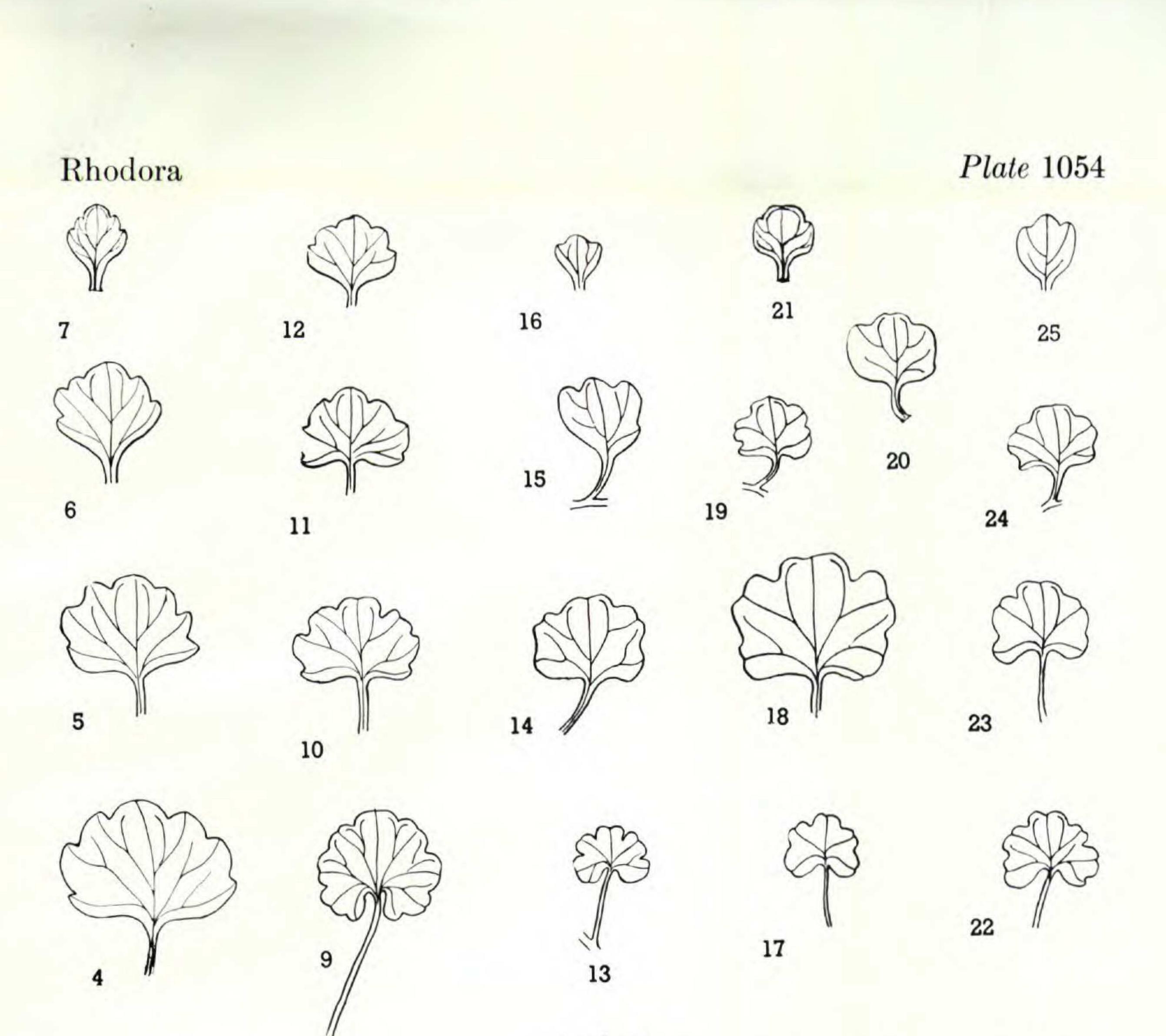
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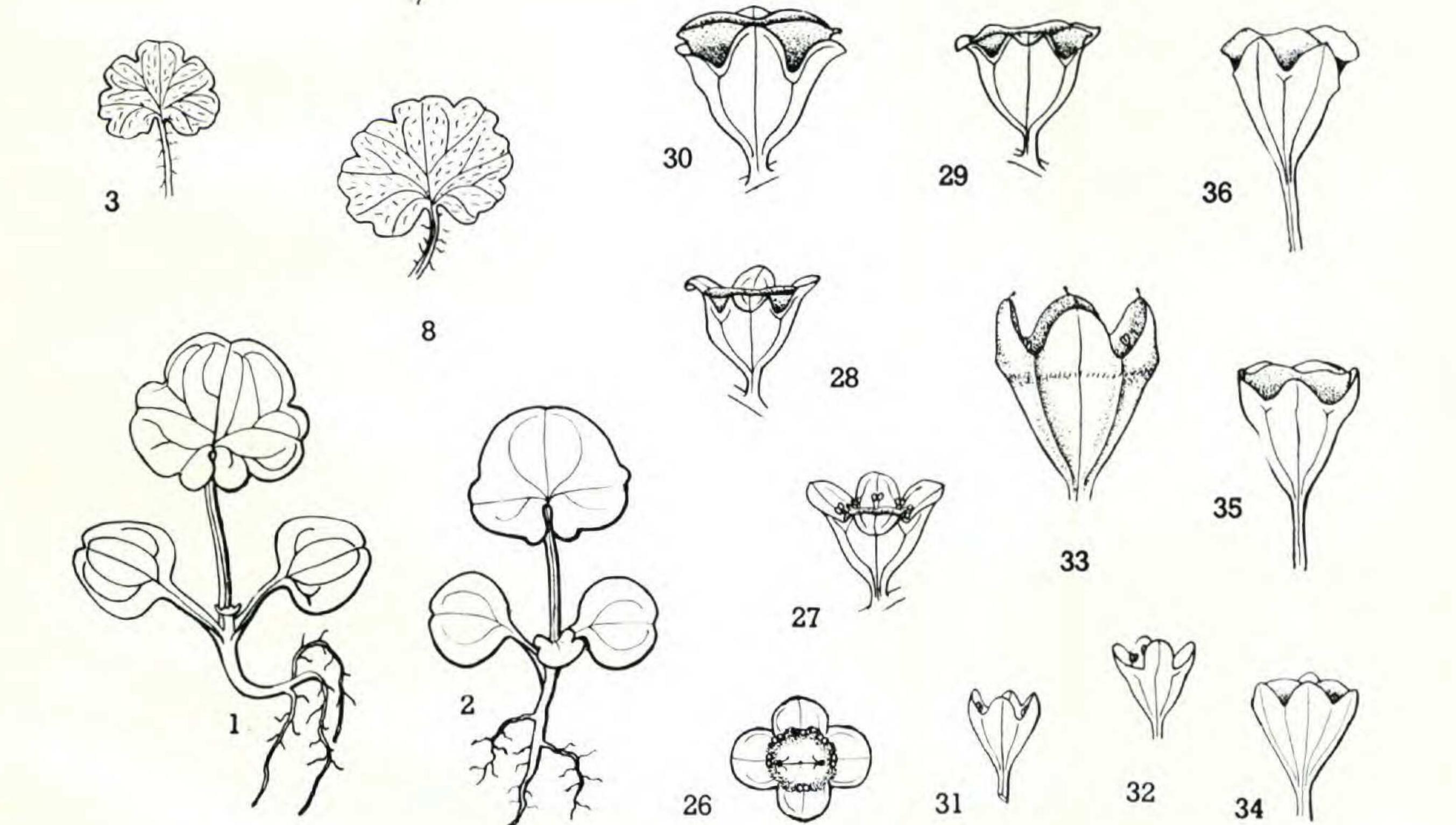
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On re-examining the Alberta specimen more thoroughly and comparing it with collections from the type locality in Iowa, I found that it matched the latter not only in the stamen character but in several additional details of flower and fruit structure as well as vegetatively. Although it appeared almost certain that the plant in question could not be anything else than Rydberg's species, yet this meant such a great gap in distribution that I hesitated to commit myself on the basis of only a single specimen. Accordingly I wrote to Professor Moss and asked if perchance he had additional specimens I might see. He kindly responded by sending me five sheets, representing four additional stations, all from within a radius of about 100 miles of Edmonton. All the collections proved to be the same entity and beyond any doubt they belonged with C. iowense. However, I was to find out from one of these sheets that the discovery had already been made but apparently left in limbo. The particular sheet is from the herbarium of C. H. Turner and contains two of his collections (No. 471 and 1670) from Fort Saskatchewan, Alberta. It is extensively annotated and the notes are sufficiently illuminating to warrant reproducing in full. The label in the lower right hand corner bears the legend: "Golden Saxifrage, Water Carpet. Chrysosplenium tetrandrum Th. Fries. Collector C. H. Turner, No. 471. Wet grounds, Sandhills Ft. Saskatchewan, Alberta June 7, 1935". A line is drawn through the species name and right below it is printed in ink iowense Rydb. This name is also crossed out and above both the scratched names is written for a second time tetrandrum Fries. There is no signature to show who made these alterations nor is it clear if they were made by one and the same person. It appears likely however, that they are to be attributed to Dr. W. P. Fraser because above the label there is attached a typewritten note by him which reads as follows: "Chrysosplenium iowense Rydb. C. tetrandrum Fries. Following Rydberg's Key some of our collections fall into this species but from a limited study of the few collections I have

made I have grave doubt if it is a good species. It is one of Rydberg's species and as far as I know has not been revised or commented on by any other botanist. It is for you to decide which to use. I'll give more attention to collections but we do not have much of it on the prairies. It is more common in the





DETAILS OF CHRYSOSPLENIUM IOWENSE and C. TETRANDRUM: FIGS. 1, 3–12 and 26–30 C. IOWENSE, FIGS. 2, 13–25 and 31–36 C. TETRANDRUM.

north." The note is dated April, 1940. Above this note there is attached another strip of paper on which is typed "1670 *Chrysosplenium tetrandrum* Fries", underneath which is written, Dr. Hugh M. Raup, Mar. 10, 1941. There are altogether eight plants on the sheet, four of which are numbered 471 and the others 1670. They are all the same entity and I assume that Dr. Raup's identification is meant to apply to both of Turner's

collections.

One can readily understand Dr. Fraser's dilemma when one recalls how difficult it often is to get a clear concept of a species from keys and descriptions alone, especially when these are much abridged as they so often are in manuals. Without authentic material at hand the job is sometimes quite baffling and obviously Dr. Fraser had no Iowa plants for comparison. As mentioned above I likewise had been skeptical about the full specific status of *C. iowense* and some forty years ago expressed this doubt by placing it in a lower category, not however under *C. tetrandrum* but as a form of *C. alternifolium.*⁴ While this disposition was admittedly erroneous, it expressed nevertheless more nearly its true phylogenetic position.

After a prolonged study of a great deal of material⁵ of both C. iowense and C. tetrandrum, including living plants of both entities, I no longer have any doubt about the former being a distinct species. It differs from C. tetrandrum and also from C. alternifolium in a number of dependable co-ordinating characters some of which have been entirely neglected, and others the importance of which appears not to have been fully recognized. Before taking these up in detail a brief history of the species is in place. Chrysosplenium iowense was first collected by Professor E. W. D. Holway in 1888 near Decorah, Iowa. The first published account of it appeared two years later in the sixth edition of Gray's Manual where it was referred to the Old World species Chrysosplenium laternifolium L. Its distribution in America was there given

⁴ Engler's Bot. Jahrb. 37: Beibl. 83, p. 86. 1905.

⁵ In addition to the Canadian material of *C. iowense*, I have had access to practically all known collections of it from Iowa including the type. I have also seen all the sheets of *C. tetrandrum* preserved in the Gray Herbarium, the New York Botanical Garden and the herbarium of the University of Minnesota. I wish to express my appreciation to Dr. Moss, Dr. Fernald, Dr. Gleason and Dr. Hayden for the loan of material.

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as "Decorah, Iowa, west to the Rocky Mts. and north through Brit. Am." Seven years later Dr. J. N. Rose⁶ published a preliminary revision of the North American species of Chrysosplenium wherein he maintained that C. alternifolium L. does not occur in America and that American material referred to it belonged instead to C. tetrandrum Fries. He furthermore stated that after the study of much material he was forced to restore the latter to specific rank despite the fact that recent monographers had considered it only a variety of C. alternifolium. The range of the species was given briefly as "Arctic regions, in America as far south as Colorado". He elaborated upon this short formal statement by adding that in the United States there are only two stations recorded for the species. One of these is in Colorado, where the plant had been collected in 1862 by Hall and Harbour (No. 576) and has not been found since, and the other at Decorah, Iowa, where Prof. E. W. D. Holway had collected it a number of times. He suggested that the plant from the latter place might prove a distinct form since it differed in being somewhat larger, with slightly different leaves and with six or seven stamens. Four years later Dr. Rydberg l. c. segregated the Iowa plant as a distinct species, giving it the name C. iowensis and pointed out that it had been "confused with C. alternifolium L. with dull punctate leaves with truncate lobes and C. tetrandrum Fries with thick 3–5-lobed leaves and 4 stamens". In his treatment of the Saxifragaceae in the North American Flora (Vol. 22: Part 2, 83. 1905) Dr. Rydberg corrected the gender of the epithet to iowense. The same year appeared my paper on the North American Saxifragaceae 1. c. where I committed the before-mentioned blunder of treating it as a form of C. alternifolium. Finally in the seventh edition of Gray's Manual it is referred without any qualifying comments to C. tetrandrum Fries and therefore presumably held to be conspecific with the latter.

It is understandable that the independent status of C. *iowense* should have been questioned at the time considering how exceed-

ingly little material was available and how little was actually known about it. Dr. Rydberg had only the two plants of the original collection before him when he drew up his description and these either did not reveal or else he failed to recognize as of *Bot. Gaz. 23: 274-276. 1897.

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diagnostic importance a number of additional stable characters which distinguish it from C. tetrandrum. The situation was not improved by his treatment in the North American Flora l. c. for there, except for the two characters he used in the key, i. e. difference in the number of stamens and lobes of the leaves, the descriptions read so much alike that one would be justified in questioning whether the two were really distinct entities. There is however no lack of differentiating characters and it seems strange that such obvious differences in flowers and leaves as are clearly shown in the accompanying photographs (Plate 1053) were not made use of. As early as the seedling stage differences between the species are manifest (Plate 1054, figs. 1, 2). By the time the plants have attained the flowering stage the contrast between them is so marked that mere outward appearance suffices to set them apart as well defined species (Plate 1053, figs. 1-6). In my experiments with growing the plants I find that C. tetrandrum produces flowers and matures seed in one season (3–4 months). During the period of active growth several leafy stolons are produced in the axils of the radical leaves. C. iowense on the other hand does not develop flowering stems the first season but produces instead a number of radical leaves and stolons. If the latter continue to grow at or close below the surface of the ground they bear a variable number of ordinary green leaves, but when they penetrate deeper their leaves are reduced to the sheathing colorless portion of the petiole and a rudimentary lamina. That the plant behaves the same in nature is indicated by the fact that in all herbarium specimens where I could make out the connection each flowering stem was found to arise from the end of a stolon of the previous season. The radical and stolon-leaves are orbicular-reniform, 7-11-lobed, with a narrow or closed basal sinus due to the overlapping of the basal lobes (Plate 1053, fig. 4; Plate 1054, figs. 3, 8). The blades are rather thin and impressed-veined above and either glabrous or sparingly pubescent on the upper surface; the stolon-leaves are pubescent (Plate 1053, figs. 1, 4; Plate 1054, figs. 3, 8) with erect white hairs on both surfaces, those on the lower side are shorter and less numerous; the lowermost cauline leaf is roundreniform to reniform (Plate 1054, fig. 9), 7-9-lobed and glabrous; the succeeding cauline leaves are flabellate, 6-7-lobed and glabrous

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(Plate 1054, figs. 4, 5, 6, 10, 11), the two uppermost are adnate by their petioles to the branches of the dichasial cyme and stand immediately underneath the inflorescence (Plate 1053, figs. 1, 2, 3). The bracts are mostly broadly obovate, 3-5-lobed (Plate 1054, fig. 7), rarely 6-lobed, and lemon-yellow in color at anthesis. In C. tetrandrum the radical and stolon-leaves are reniform, 5-7-lobed, with a rather open basal sinus (Plate 1053, fig. 5; Plate 1054, figs. 13, 17, 22), thick and glabrous except for a sparse pubescence of crinkly hairs on the petioles, sometimes a few of these hairs extend up on the edges of the basal lobes and very rarely stolon-leaves are found with a few hairs on the surface of the lamina toward the base. The lower and middle cauline leaves are subreniform or often with a truncate base and nearly parallel sides (Plate 1054, figs. 14, 18, 23), 5-lobed and glabrous; the two uppermost are irregularly 4-5-lobed, somewhat variable in shape (Plate 1054, figs. 15, 19, 20, 24), and with less regular adnation of their petioles to the cyme-branches. The bracts are obovate, mostly with broadly cuneate base, and 3lobed to entire (Plate 1054, figs. 16, 21, 25). The flowers in C. iowense are bright golden-yellow, shortcampanulate (Plate 1054, fig. 27) and 3.5-4.5 mm. broad at anthesis; the sepals are spreading, with recurved tips (Plate 1053, figs. 2, 3), those of the outer cycle considerably broader than long and obtuse at the apex, the two of the inner cycle somewhat narrower and less bluntly rounded (Plate 1054, fig. 26), all more or less distinctly 3-nerved; disk narrow, stamens 8-5, mostly 7-6, 0.6-0.7 mm. long, styles 0.3-0.4 mm. long; mature fruit campanulate (Plate 1054, figs. 29, 30), the mouth of the dehiscing capsule even with or slightly exceeded by the sepals; the seeds are ellipsoid, 0.7-0.8 mm. long and dark reddish-brown when fully mature.

The flowers of *C. tetrandrum* are green or rarely faintly yellowtinged, often spotted with anthocyanin, turbinate (Plate 1054, figs. 31, 32, 33), 2–2.5 mm. broad at anthesis; sepals erect, convexo-concave, with the margins and rounded tips incurved (Plate 1053, fig. 5, Plate 1054, fig. 33), all four of nearly equal size, obscurely 1-nerved, the lateral nerves either lacking or showing faint traces near the base only; disk obsolete; stamens 4, rarely 3, 0.3–0.4 mm. long; styles 0.2–0.25 mm. long; mature

fruit trumpet-shaped, the flaring mouth of the capsule overtopping the sepals (Plate 1054, fig. 36); seeds ovoid, 0.6-0.7 mm. long, bright chestnut-brown.

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The principal distinguishing differences may be summarized as follows:

Flowers short-campanulate, 3.5-4.5 mm. broad at anthesis: sepals bright yellow, spreading, with recurved tips, the two outer noticeably broader and blunter than the two inner and clearly 3-nerved; stamens 8-5, mostly 7-6, 0.6-0.7 mm. long, filaments about twice as long as the anthers; seeds dark reddish-brown; radical and stolon-leaves orbicular-reniform, 7-11-lobed, stolon-leaves pubescent on both surfaces, upper and middle cauline leaves flabellate, mostly 6-7-lobed, bracts Flowers turbinate, 2-2.5 mm. broad at anthesis; sepals green, sometimes faintly tinged with yellow, often with purplish spots, erect with incurved sides and tips (convexo-concave), all four of nearly equal size, obscurely 1-nerved; stamens 4, 0.3–0.4 mm. long, filaments shorter than the anthers; seeds bright chestnut-colored; radical and stolon-leaves reniform, 5-7-lobed, glabrous, except for sparse pubescence on petioles, upper and middle cauline leaves from broadly obovate to subreniform, more or less irregularly 3-5-lobed, bracts green. . . . C. tetrandrum

Although, as already suggested, C. iowense stands closer phylogenetically to C. alternifolium than to C. tetrandrum, it is nevertheless amply distinct from the common Old World species. One of the characters which both Rose, l. c., and Rydberg, l. c., regarded as diagnostic for C. alternifolium is the spotted or dotted nature of the leaves and sepals. These dots are due to the presence of internal tannin cells which occur either singly, or more often, in smaller or larger groups. In occasional herbarium specimens they are not very obvious, but by treating with ferric chloride they turn black and stand out conspicuously. I have not found any specimens of C. alternifolium from its entire range in Europe in which these tannin cells are lacking. In striking contrast they are entirely absent in all the material of both C. iowense and C. tetrandrum which I have studied. In the original description of C. tetrandrum Fries⁷ described the sepals and also the carpels as being brown-dotted. In many specimens of the species, especially from the far north, the sepals, carpels and sometimes the bracts and leaves also are spotted, but here the spots are due to the presence of anthocyanin in small patches of epidermal cells and they are reddish or purplish instead of brown.

⁷ Fries, Th. M. Bot. Notiser. p. 193. 1858.

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They disappear completely by boiling or merely soaking in water, whereas the dots in C. alternifolium are a permanent feature, unaffected by boiling or treating with alcohol. When, in addition to a fundamental and unmistakable anatomical character of this kind, there are a number of stable correlating characters of flower⁸ and foliage which set off C. alternifolium sharply from C. tetrandrum, it is difficult to understand why the latter has come to be regarded by many as a mere variant of the former. In raising it to specific rank, Fries, l. c., showed a better understanding of the plant than did either Maximowicz⁹ or Franchet¹⁰, the two chief monographers of the genus, and those who have followed them in treating it only as a variety. Fries knew the two entities in the field and he remarked that when he first encountered C. tetrandrum on a journey in Finmarken after having observed C. alternifolium in "full splendor" all the way through Guuldalen, he was impressed by their marked dissimilarity. He moreover emphasized that they had entirely different geographical distributions.¹¹

The persistence, especially of European systematists (Hegi, Mittel Eur. Flora 4: 2, 635; Engler & Prantl, Ed. 2, 18a, 164. 1930) in treating *C. tetrandrum* as only a variety is no doubt largely due to Simmons', l. c., categorical statement that if sufficient material is examined the "arctic and temperate forms will be seen to be continually connected by intermediate forms". His principal argument for this dictum is the occurrence in the Arctic of plants with stamens varying in number from 4–8. He further sought to strengthen the case by maintaining that there are intermediates in respect to stature and shape of leaves. Size of plants is altogether too variable in either species to be of any significance and leaf-form is of lesser importance unless strictly corresponding leaves are compared.

⁸ The flowers of *C. alternifolium* are short-campanulate, 5–6 mm. broad at anthesis; the sepals are golden yellow, spreading, recurved at the tips and 3-nerved; there is a broad nectariferous disk, regularly 8 stamens which are more than twice as long as in *C. tetrandrum*, and the styles are fully three times as long. The radicle leaves are orbicular to orbicular-reniform, 11–16-lobed (most commonly 13). The lobes are truncate or more or less deeply emarginate, with nearly straight parallel sides, giving them a rectangular to broadly cuneate shape; the thin blades are conspicuously publescent on both surfaces.

⁹ Maximowicz, A. J. Melanges Biol. IX: 762. 1876.

¹⁰ Franchet, M. A. Nouvelle Archives d'hist. Nat. 3 Ser. II, 1890.

¹¹ The northernmost recorded station for C. alternifolium is at Overhalden, Norway, Lat. 64° 30' N., while the southernmost occurrence of C. tetrandrum in Europe is around Lat. 67° 30' N. in Sweden.

I have searched assiduously for these purported intermediates and I am unable to find any. The scores of plants of C. tetrandrum which I have raised from seeds from several collections made by Miss Oldenburg in the American Arctic are remarkably uniform as regards both the vegetative and reproductive tracts. I have not encountered a single individual which shows any degree of variation either toward C. alternifolium or C. iowense. The same is equally true of all the herbarium material I have studied. The plants Simmons and others have mistakenly held to be intermediate forms prove instead to be another and distinct entity, which on no other character than the variable number of stamens can be claimed to be intermediate. This entity, with prevailingly 6-7 stamens is in my opinion C. iowense. As long as the latter appeared to be restricted in its distribution to a limited area in northeastern Iowa, this assertion might well be open to serious question, but as already shown, it is not so limited in its range. Not only does it occur in a number of places in Alberta, but it also appears to be widely distributed in the Arctic. I have one collection made by Miss Oldenburg at Cambridge Bay, Victoria Island, which in flower, fruit and seed characters matches C. iowense completely. Only in its smaller size (3-6 cm.)and smaller, somewhat fleshier leaves does it differ from specimens from Iowa. I would also refer to the same species a collection by Ralph Robinson (No. 42) from Cairn Lake, Baffin Island. It is a moldy and poorly preserved specimen, but it has the open larger flowers with more than 4 stamens characteristic of the species. In Gröntved's¹² paper on the Vascular Plants of Arctic North America there are listed several collections of Chrysosplenium, three of which are reported to have 6 or 7 stamens. While I have not had access to these specimens, I am of the opinion that they are not C. tetrandrum but low Arctic forms of C. iowense. From the Old World Arctic I have seen two collections which I believe belong with the latter also. One is from the Island of Vaigach by Otto Ekstam, the other from near the mouth of the Yenisei (Lat. 72° 25' N., Long. 80° 35' E.) by N. J. Kusnezow and W. W. Reverdatto. Both collections are identified as C. alternifolium which they clearly are not. They lack the charac-¹² Gröntved, Johs., Report of the Fifth Thule Expedition 1921-24 Vol. II, No. 1.

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teristic tannin cell dots and they have glabrous radical and cauline leaves. Some of the flowers have 8 stamens and these as well as the styles are of the same length as in C. iowense. The Ekstam specimen has the ellipsoid, dark reddish brown seeds and pubescent stolon-leaves characteristic of the latter. In presenting evidence for retaining the varietal status of C. tetrandrum, Heintze, I. c., reported finding plants at Saarikoski, Torne Lapmark, in 1904 with "stems up to 1 dm. high, very succulent, lower leaves pubescent, of the size of the head species, occasional flowers with 8 stamens". Three years later he described in detail plants from the same locality, stating that the lowermost stem-leaves were glabrous or sparsely hairy and the stolonleaves were always pubescent, with the hairs distributed evenly and richly over the surface. The stamens were reported as 4 or seldom 3. I am inclined to doubt if Heintze was dealing with strictly one entity, for I have never yet found such a combination of characters in C. tetrandrum as he records. His failure to make any mention whatever of the basic differences in the shape of the flower of the two entities is also a little suspicious.

While it is obviously not safe on the present evidence to assert that C. iowense or a variant of it occurs in the Old World Arctic, it is certain that a form occurs there which is neither C. alternifolium nor C. tetrandrum and that this form does agree in floral and vegetative characters with C. iowense as it occurs in the American Arctic. Possibly this form should be treated as an arctic variety but the study of more material needs first to be made. The isolated occurrence of the species in northeastern Iowa presents a striking case of disjunct distribution and another instance of a Pleistocene relic holding out in or on the edges of the Driftless Area. It is mostly limited to cold-water seepage places on north-facing wooded bluffs. At Brainard in Fayette County it grows at the entrance to an ice cave and in Pine Hollow, Dubuque County, at the entrance to a cool cave. The type locality has been given as Decorah but this is an error. The actual site is in the Canoe Creek Valley, six miles due north of Decorah.

In citing specimens the following abbreviations have been used: G., Gray Herbarium; I. S. C., Iowa State College; M.,

and that the same

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University of Minnesota; N. Y., New York Botanical Garden; U. A., University of Alberta; U. I., University of Iowa.

The following specimens of C. iowense have been examined: IOWA: Sect. 8, Canoe Twp., WINNESHIEK Co., in moss, July 1, 1888 (G., type), May 5, 1889 (I. S. C.), May 1893 (I. S. C.), E. W. D. Holway; same station, May 31, 1889 (M.), May 17, 1900 (M.), June 10, 1900 (M.), A. F. Kovarik; same station, Aug. 4, 1919 (M.), C. O. Rosendahl Nos. 3852, 3853; Decorah, May 5 and June 16, 1899 (I. S. C.), Herbert Goddard; Sect. 6, Decorah Twp., May 17, 1933 (I. S. C.), May 28, 1934 (I. S. C.), W. L. Tolstead; same station, growing in Mnium moss on moist talus, May 15, 1946 (M.), C. O. Rosendahl No. 7763; same station, May 29, 1946 (M.), Rosendahl, Moore and Huff No. 7764; entrance to ice cave, Brainard, Pleasant Valley Twp., FAYETTE Co., June 10, 1899 (M., I. S. C.), A. F. Kovarik; Pine Hollow State Park, Sect. 6, Liberty Twp., DUBUQUE Co., June 16, 1940 (I. S. C.), Ada Hayden No. 9902; same station, growing on rocks at mouth of cold cave, June 27, 1946 (M.), Dietz, Barret and Young; wooded bluff oposite Old Stone House, ALLAMAKEE Co., June 24, 1929 (U. I.), B. Shimek. ALBERTA: Elbow River, Rocky Mts., Lat. 49° 40', June and July 1897 (G., N. Y.), John Macoun No. 20168; forest edge, 100 miles N. of Edmonton, May 15, 1915 (U. A.), C. H. Turner; east of Edmonton, May 25, 1919 (U. A.), W. C. McCalla No. 2665; wet places, poplar spruce grove, near Edmonton, May 26, 1926 (U. A., M.), E. H. Moss No. 280; near Edmonton, June 7, 1926 (U. A.), E. H. Moss No. 365; wet Sphagnum bog, fed by iron spring, north of McLeod Valley, about 120 miles west of Edmonton, July 21, 1945 (M.), E. H. Moss No. 6821; damp mossy ground under willows, near Peers, about 120 miles west of Edmonton, July 24, 1945 (M.), E. H. Moss No. 6864; Fort Saskatchewan, June 7, 1935 (U. A.), C. H. Turner No. 471; Sand Hills, 8 miles N. E. of Fort Saskatchewan, May 27, 1940 (U. A.), C. H. Turner No. 1670; low, wet forest trail, 9-mile point, Slave Lake District, May 31, 1929 (N. Y.), A. H. Brinkman. DISTRICT OF FRANKLIN: wet drainage valley, Cambridge Bay, Victoria Island, Aug. 18, 1944 (M.), Margaret E. Oldenburg No. 921; shore, Cairn Lake, Baffin Island (G.), July 28-30, 1922, Ralph Robinson No. 42.

